

BIOLOGICAL OBSERVATIONS ON AN OVERWINTERING
COLONY OF MONARCH BUTTERFLIES (*DANAUS*
PLEXIPPUS, DANAIIDAE) IN MEXICO

LINCOLN P. BROWER,¹ WILLIAM H. CALVERT,²
LEE E. HEDRICK,¹ AND JOHN CHRISTIAN³

On 31 December 1976 we independently located a massive overwintering colony of monarch butterflies (*Danaus plexippus* (L.)) in the mountains of the state of Michoacan, Mexico, at a locality which we designated as Site Alpha (Brower, 1977). Our independent confirmation of Urquhart's (1976) and Urquhart & Urquhart's (1976) original discovery provides proof for the extensive nature of the monarch's migration. This behavior had long been inferred from the large southward migration in the fall (Williams, 1930; Urquhart, 1960) together with year to year fidelity to specific overwintering sites in California (Williams et al., 1942). Prior to the Urquharts' discovery, the alternative hypothesis of a continuously breeding population in the overwintering range followed by northward dispersal in the spring could not be ruled out (Brower, 1961, 1962; Urquhart et al., 1970; Schmidt-Koenig, 1975).

In this paper we present results obtained during an expedition to Site Alpha on 22–27 January 1977 which bear importantly on several aspects of the biology of the monarch butterfly.

Geography and Vegetation of Site Alpha

Site Alpha is near the continental divide in a montane coniferous forest on the north facing slope of a northeast–southwest running ridge. Using a Thommen altimeter and a 1:50,000 topographic map, we determined that the ridge drops from an altitude of 3180 m over an average slope of 29° to the upper reaches of a small creek, at about 2960 m. Based on compass sitings and measurements, the colony was approximately 100 × 150 m or 1.5 ha (3.7 acres) in area. Altitudes of upper and lower boundaries were approximately 3120 and 3050 m, without apparent topographic determinants. The west and east sides were bounded, respectively, by a draw and a logging cut both about 10 m wide.

The forest, which is not virgin, is dominated by three species of conifers, the fir *Abies religiosa* H.B.K. (also called "Oyamel"), the cypress *Cupressus lindleyi* Klotzsch, the pine *Pinus ayacahuite* K. Ehren., and two

¹ Department of Biology, Amherst College, Amherst, Massachusetts 01002.

² Department of Entomology, University of Massachusetts, Amherst, Massachusetts 01003.

³ P.O. Box 13285, Austin, Texas 78711.

TABLE 1. Frequency and diameters of the major trees species in the overwintering colony of monarch butterflies at Site Alpha, Michoacan, Mexico. January 1977. (The diameters are based on the nearest neighbor sample only.)

Tree Species	% of tree species in:				Diameters (m)	
	Nearest Neighbor Sample ¹	Transect Samples ²		Mean %	Mean	Range
		1	2			
<i>Abies religiosa</i>	63	54	57	58	0.21	0.04-0.46
<i>Cupressus lindleyi</i>	13	18	14	15	0.18	0.08-0.54
<i>Pinus ayacahuite</i>	17	4	6	9	0.26	0.06-0.77
Broadleaf spp.	7	24	22	18	0.17	0.05-0.39
Sample sizes (N)	100	28	49	177	100	100

¹ Includes trees ≥ 10 cm DBH.

² Includes trees < 10 cm DBH.

small broadleaf trees (Table 1). In addition, there is a fairly sparse understory of small shrubs including *Senecio angulifolius* D.C., the herb *S. prenanthoides* A. Rich. (Sanchez, 1976), and a lush carpet of moss including one or more species in the genera *Thuidium* and *Mnium*. Other mesic indicators growing on the forest floor, on rocks, or as epiphytes included lichens (*Usnea* and *Peltigera*), and ferns (*Asplenium* and *Adiantum*).

Tree density was estimated by the nearest neighbor technique ($N = 100$) and by two transect samples ($N = 28$ and 49) across the central area of the colony showing, respectively, 1830, 2805, and 2490 trees ($\bar{x} = 2375$) in the 1.5 ha occupied by the butterflies. These values differ from Urquhart's (1976) and Urquhart & Urquhart's (1976) estimate of 1000 trees in a colony of 20 acres (8.1 ha) given for the previous year. The relative abundance of the trees is shown in Table 1. Firs not only dominate the forest numerically, but based on separate measurements made in one dense cluster area, are the largest and tallest of the species (Table 2).

Many of the trees were so heavily laden with butterflies that it was

TABLE 2. Heights and diameters of a sample of trees containing very dense butterfly clusters. (Heights were determined by means of a Haga altimeter.)

Tree Species	Sample Size	Heights (m)		Diameters (m)	
		Mean	Range	Mean	Range
<i>Abies religiosa</i>	11	20.3	15-29	0.29	0.14-0.55
<i>Cupressus lindleyi</i>	5	12.1	8-21	0.21	0.10-0.42
<i>Pinus ayacahuite</i>	3	11.3	9-13	0.27	0.25-0.29

TABLE 3. Density of clusters upon a random sample of 100 trees in the colony center. A score of 1 denotes a tree with no butterflies, and a score of 5 denotes clustering of extremely high density.

Tree Species	No. of trees of each cluster density					Mean Scores
	1	2	Score 3	4	5	
<i>Abies religiosa</i>	2	21	17	13	10	3.13
<i>Cupressus lindleyi</i>	0	0	0	6	7	4.54
<i>Pinus ayacahuite</i>	1	4	3	7	2	3.29
Broadleaf spp.	0	5	1	1	0	2.43

difficult to see their leaves. Relative density was estimated by scoring from 1 to 5, i.e., from none to a very heavily laden tree (Table 3). The densest clusters were on the cypress trees, which were often bowed over under the weight of the butterflies. The scaly foliage of these trees seemed to provide the best foothold. Both pine and fir offered the butterflies much more surface area than the broadleaf trees.

Clustering Behavior and Climatic Conditions

The vertical distribution of monarchs in the forest appeared adapted to avoiding wind, frost, and snow. Wind velocities were near zero at all times in the lower parts of the trees where the butterflies were concentrated. However, in the treetops (as was also true along the ridge), wind velocities were frequently considerable and the tallest trees projecting above the canopy were devoid of roosting butterflies. Clusters less than 2 m from the ground also were rare, presumably indicative of an adaptation to avoid ground level freezing temperatures and snow-fall which have been reported in the area (Urquhart & Urquhart, *l.c.*, Kenneth Brugger, pers. comm.).

We used two sets of thermometers (Taylor Max-Min) to measure the temperature range over the period of 22–27 January at heights of approximately 0, 5, and 10 m above the ground. Minimum temperatures ranged from 5.6°–8.9°C, and maximum from 13.3°–15.5°C. This thermal stability was particularly striking in that weather conditions during our stay included brilliantly clear, partly cloudy, and overcast days. In a nearby clearing, only about 70 m higher in altitude than Site Alpha, the dawn temperature on 23 January was 0°C and the relative humidity 100%. Heavy frost was on the ground in the open area of the clearing, but did not occur under the adjacent trees. In contrast, the minimum for the same day in the colony was 6.1°C, indicating the moderating effect of the forest.

Estimated Number of Overwintering Butterflies

A crude estimate of the total monarch butterflies at Site Alpha is possible by comparison with California overwintering colonies. Tuskes & Brower (1978) utilized a mark, release, and recapture method in a *Eucalyptus* overwintering grove of about 1000 m² (1 ha) at Santa Cruz, and estimated a peak abundance of 95,000 butterflies. A colony at Muir Beach occupied a smaller area of Monterey pines (*Pinus radiata* Don.) and had a maximum of 40,000 butterflies. Visual estimates of the monarchs on the California trees at both sites suggested a density of less than one tenth that observed in Mexico. By multiplying the differences in the area (15×) and butterfly density (10×) for Mexico, times the number of butterflies at Santa Cruz (95,000), we obtained a value of 14.25 million butterflies at Site Alpha. We believe this to be a conservative estimate.

Critical Nature of the Temperature at Site Alpha

Our observations indicated that the maximum shade temperature at the site was near the critical threshold (15–16°C) at which flight in the monarch is possible (Kammer, 1970). On partly cloudy days, short sunny periods elicited extensive openwinged basking in the trees. This behavior facilitates a rapid rise in thoracic temperature of the monarch butterfly (Kammer & Bracci, 1973) and greatly reduces its preflight warm-up time (Wasserthal, 1975). We noted that even short periods of sunlight resulted in a pullulating flight activity above the forest. When cloudiness followed, this changed from soaring to rapid fluttering as the butterflies rejoined existing clusters (Brower & Huberth, 1977). This sudden alteration in behavior was audibly noticeable because of the great numbers involved. It seems likely that cluster reformation involves both visual and pheromone cues released by the butterflies as they aggregate.

The critical nature of the temperature became evident in the behavior of butterflies dislodged from their roosts. Cattle, grazing on forest foliage and fallen butterflies, often knocked against roost trees, causing the butterflies to spill onto the ground by the hundreds and sometimes thousands, as did smoke from a small fire set by a local rancher. This latter event was preceded by a long overcast period with the temperature at about 13°C, and at least 10,000 dislodged butterflies flapped helplessly on the ground (Fig. 1) until settling into a prolonged period of thermoregulatory shivering (Kammer, 1970, 1971). Many were unable to raise their thoracic temperatures to the point where they could

fly back to a cluster. However, by the next morning nearly all had crawled upward, from a few centimeters to a meter, into vertical positions on rocks and small plant stems (Fig. 2).

Reproductive Diapause and Mating Dynamics

The ratio of males to females was determined from two samples of the smoked-down butterflies. The first sample, made immediately after the incident, indicated no significant excess of one sex over the other (53% females, $N = 480$; $\chi^2_1 = 1.64$, $P > 0.20$). The sample made the next morning, with a bias for those that had crawled up the highest from the ground, showed a significant excess of females (57% females, $N = 509$; $\chi^2_1 = 9.90$, $P < 0.005$). These figures suggest that differential behavior of the sexes can lead to inaccurate estimates of the sex ratio and should be kept in mind when attempting to estimate sex ratios in the field.

The colony was largely in reproductive diapause. Less than a dozen mating pairs were seen and, based on the technique of Burns (1968), dissection of 111 females indicated that 85% were virgins (Table 4). Moreover, there was no indication of mature or maturing eggs in the entire sample. Lowered sexual activity in overwintering monarchs has long been known from studies in California overwintering sites (Williams et al., 1942), but the dynamic nature of within-colony mass mating has only recently been described (Hill et al., 1976). On the California coast near Santa Barbara (latitude approximately 34°N), the frequency of mating in one colony built up from sporadic occurrences in mid-January to spectacular proportions by mid-February, after which the colony broke up. Similar behavior was also observed previously at Site Alpha (Brugger, pers. comm.). According to Urquhart & Urquhart (1976) mating at the Mexican site was frequent on 24 January 1976, a warm day (22°C), but by 9 February the colony had mostly dispersed. It appears, therefore, that there is a behavioral uniformity of the mating dynamics in the Mexican and Californian overwintering colonies. If the monarch assemblage at Site Alpha is in fact comprised of butterflies from across the eastern North American breeding range, then this mass colony mating behavior must have a profound homogenizing effect upon any genetic divergence which might take place during the geographically disparate breeding cycles of the summer.

Physiological studies of the neuroendocrine control of reproductive diapause in male and female monarchs indicate that both daylength and temperature are involved (Barker & Herman, 1973, 1976; Herman, 1973, 1975; Pan & Wyatt, 1976). Although high temperature to a cer-

TABLE 4. Mating status and free lipid content of a sample of 111 females collected at Site Alpha on 25–26 January 1977.

No. of spermatophores in bursa				Free lipids in abdomens		
0	1	2	3	None	Moderate	Considerable
85%	11%	2%	2%	24%	39%	37%

tain extent can override short daylength, oögenesis is minimal to absent at daylengths of less than 11–12 h and temperatures of less than 20°C (Barker & Herman, 1976). Site Alpha is at approximately 20° North Latitude where at winter solstice the light period is 10 h 48 min (Finch & Trewartha, 1949). By 1 February, daylength would be critical, i.e., ca. 11.3 h (Beck, 1968), with the stage set for the massive panmictic mating ceremony to be triggered by rising temperatures.

We obtained experimental evidence in support of this thermal triggering hypothesis. Fifteen females and 14 males collected at Site Alpha on 27 January were taken to Amherst, Massachusetts and placed in nylon cages the following evening in a controlled environment room at 22–30°C and 75–81% relative humidity. By 31 January, with only two days of exposure to the 15 h light period, 9 of the 15 pairs had mated.

These physiological findings are in remarkable agreement with the observations on spring and summer breeding dates and range of the monarch in eastern North America (Urquhart, 1960; Williams et al., 1942). Since oögenesis occurs slowly at low temperatures and does not peak until 28°C (Barker & Herman, 1976), the mated females are free to leave the colony and migrate northward initially unencumbered with large numbers of eggs, but with an increasing rate of egg maturation as both seasonal temperature and daylength increase.

Robust Condition of the Butterflies

The general appearance of the majority of monarchs at Site Alpha was of exceptionally high quality compared to butterflies from overwintering sites in California (Tuskes & Brower, *l.c.*). Few butterflies were tattered and the abdomens of most appeared robust. The dissection sample indicated that three-fourths of the females had moderate to considerable amounts of free lipids (Table 4) and well developed fat bodies (Brower, Calvert & Hedrick, ms in prep.) as is characteristic of fall migrants (Beall, 1948; Cenedella, 1971; Brown & Chippendale, 1974). The butterflies also appeared to be in a favorable state of water balance. On the clear days we observed them flying down along the draw to the



Fig. 1. Thermoregulatory struggle of more than 10,000 monarch butterflies which released their grip in response to smoke from a small fire (less than one meter in diameter) which drifted laterally and upwards through the clusters in the trees. The ambient temperature in the forest was about 13°C at the time of the incident (ca 1500), 2°C below the thoracic temperature at which monarchs are able to fly. Original 35 mm Kodachrome by George D. Lepp.

creek and many thousands were drinking at moist spring sites and along the creek itself.

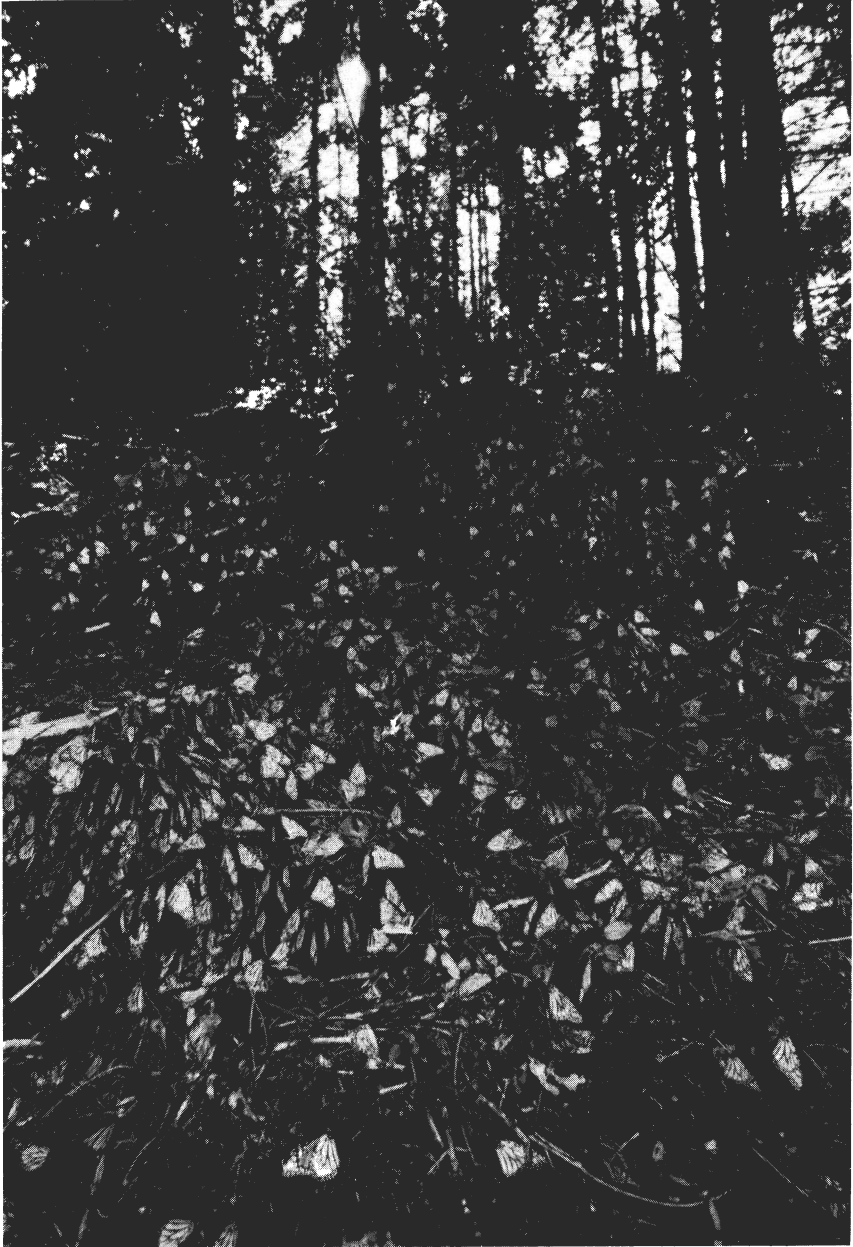
Nectaring was observed on several flowering herbs and shrubs, including at least one species in the genus *Bidens*, two in *Lupinus*, four in *Senecio*, and two in *Stevia*. However, the numbers of butterflies so vastly exceeded the available flowers in the area that nectar during their overwintering period cannot be an important source of carbohydrate.

Predation by Orioles

We also observed attacks by birds, identified with the use of Peterson & Chalif (1973). At 1120 on 26 January, a small flock of Bullock's Oriole (*Icterus bullockii* Swainson) flew into a fir tree which had no

→

Fig. 2. Because of the low ambient temperature, many of the smoked-down butterflies could not fly back to the clusters. This picture, taken the next morning,



shows them having crawled up into less vulnerable positions on projecting rocks and vegetation. By noon, the temperature had risen sufficiently and virtually all the butterflies had flown back up into the clusters. Original 35 mm Kodachrome by George D. Lepp.

roosting monarchs on it. From this tree they flew singly to an adjacent fir laden with monarchs and upon landing displaced several butterflies, which either dropped to the ground or flew off into the forest. Only clustering butterflies were attacked and the birds remained in a small area feeding upon them for about 45 min. Ingestion *per se* was not observed, but one monarch wing floated down and beak snapping could be heard frequently among the clusters. A kiskadee-like flycatcher (probably *Pitangus sulphuratus* L.) was observed perching near a cluster, but was not actually seen feeding on the monarchs. Two other patterns of apparent bird predation occurred extensively along the logging cut bordering the eastern side of Site Alpha. Numerous individual wings littered the forest floor along with many maimed but still living butterflies, including ones with one or more wings missing and others lacking their abdomens. Comparable predation has been noted in California (Kammer, 1970).

Mortality Caused by Man

Overall, natural mortality seemed to be low at Site Alpha. However, upslope from the colony, dead butterflies littered the ground to an extent that their odor of decomposition was strongly evident. Based on Calvert's observation of the upper boundary of the site on 31 December, we believe that a substantial percentage of the colony may have been eaten and trampled by cattle led to Site Alpha by local ranchers.

Likelihood of Many Overwintering Sites in Mexico

Urquhart (1976) and Urquhart & Urquhart (1976) maintained that overwintering of the monarch butterfly in Mexico is geographically restricted, involving as few as four sites in one general area. We believe that, as is the case in California (Williams et al., 1942) numerous overwintering sites will be found in Mexico at locations having ecological characteristics similar to those at Site Alpha. The principal reason for our contention is that roosting in a very limited area would make the butterflies highly vulnerable to fire. Not only does overwintering occur during the dry season, but this area of Mexico is in the Trans-Mexico Volcanic Belt (Anon., 1961). Past volcanic activity must have set many large fires which would have decimated whole colonies.

The pressing need to mount a conservation effort to preserve Site Alpha has been described elsewhere (Brower, 1977).

SUMMARY

More than 14.25 million monarch butterflies in prime condition overwinter in a 1.5 ha site located in a coniferous forest in the trans-volcanic belt of Mexico. The site is characterized by thermal stability, low wind velocity, and high humidity. The reproductive status of the butterflies and their thermoregulatory activities in the colony support conclusions from experimental physiology. Genetic implications of mass mating behavior prior to dispersal and northward migration appear great.

ACKNOWLEDGMENTS

We are grateful to the following people for help during the initial stages of our search for the location of Site Alpha: Natalie Drake, Elizabeth Mahan, Dr. Victoria Foe, Dr. Michael Dennis, Dr. Richard Lindley, Dr. Paul Tuskes, and Dr. Steven P. Lynch. We also thank Dr. Rudolf M. Schuster and H. E. Ahles for identifying the plants and Christine M. Moffitt and Helen S. Smith for critically reading the manuscript. The research was supported by a grant (DEB 7514265) from the National Science Foundation with L. P. Brower as Principal Investigator.

LITERATURE CITED

- ANONYMOUS. 1961. Tectonic map of Mexico. Geological Society of America.
- BARKER, J. F. AND W. S. HERMAN. 1973. On the neuroendocrine control of ovarian development in the monarch butterfly. *J. Exptl. Zool.* 183: 1-9.
- . 1976. Effect of photoperiod and temperature on reproduction of the monarch butterfly, *Danaus plexippus*. *J. Insect Physiol.* 22: 1565-1568.
- BEALL, G. 1948. The fat content of a butterfly, *Danaus plexippus* Linn., as affected by migration. *Ecology* 29: 80-94.
- BECK, S. D. 1968. *Insect photoperiodism*. Academic Press, N.Y. and London. viii + 288 p.
- BROWER, L. P. 1961. Studies on the migration of the monarch butterfly. I. Breeding populations of *Danaus plexippus* and *D. gilippus berenice* in south central Florida. *Ecology* 42: 76-83.
- . 1962. Biology of the monarch butterfly. *Ecology* 43: 181-182.
- . 1977. Monarch migration. *Natural History* 86(6): 40-53.
- BROWER, L. P. & J. C. HUBERTH. 1977. Strategy for survival: behavioral ecology of the monarch butterfly. 16 mm, sound, color, 30 minute film. Harper and Row, Inc., 10 E. 53rd St., N.Y. 10022.
- BROWN, J. J. & G. M. CHIPPENDALE. 1974. Migration of the monarch butterfly, *Danaus plexippus*: energy sources. *J. Insect Physiol.* 20: 1117-1130.
- BURNS, J. M. 1968. Mating frequency in natural populations of skippers and butterflies as determined by spermatophore counts. *Proc. Nat. Acad. Sci. USA* 61: 852-859.
- CENEDELLA, R. J. 1971. The lipids of the female monarch butterfly, *Danaus plexippus*, during fall migration. *Insect Biochem.* 1: 244-247.
- FINCH, V. C. & G. T. TREWARTHA. 1949. *Elements of geography*, 3rd ed. McGraw-Hill Book Co., Inc. N.Y. xii + 711 p.

- HERMAN, W. S. 1973. The endocrine basis of reproduction inactivity in monarch butterflies overwintering in central California. *J. Insect Physiol.* 19: 1883-1887.
- . 1975. Endocrine regulation of post-eclosion enlargement of male and female reproductive glands in monarch butterflies. *Gen. Compar. Endocrin.* 26: 534-540.
- HILL, F. H., JR., A. M. WENNER, & P. H. WELLS. 1976. Reproductive behavior in an overwintering aggregation of monarch butterflies. *Amer. Midl. Nat.* 95: 10-19.
- KAMMER, A. E. 1970. Thoracic temperature, shivering, and flight in the monarch butterfly, *Danaus plexippus* (L.). *Z. Vergl. Physiol.* 68: 334-344.
- . 1971. Influence of acclimation temperature on the shivering behavior of the butterfly *Danaus plexippus* (L.). *Z. Vergl. Physiol.* 72: 364-369.
- KAMMER, A. E. & J. BRACCI. 1973. Role of the wings in the absorption of radiant energy by a butterfly. *Comp. Biochem. Physiol.* 45A: 1057-1064.
- PAN, M. L. & G. R. WYATT. 1976. Control of vitellogenin synthesis in the monarch butterfly by juvenile hormone. *Developmental Biol.* 54: 127-134.
- PETERSON, R. T. & E. L. CHALIF. 1973. A field guide to Mexican birds. Houghton and Mifflin Co., Boston. xxii + 298 p.
- SANCHEZ, O. S. 1976. La flora del Valle de Mexico. 3rd ed. Printed by the author, Mexico, D.F. viii + 520 p.
- SCHMIDT-KOENIG, K. 1975. Migration and homing in animals. Springer-Verlag, Berlin. xii + 99 p.
- TUSKES, P. M. & L. P. BROWER. 1978. Overwintering ecology of the monarch butterfly, *Danaus plexippus*, in California. *Ecol. Ent.* 3: (in press).
- URQUHART, F. A. 1960. The monarch butterfly. Univ. of Toronto Press, xxiv + 361 p.
- . 1976. Found at last: the monarch's winter home. *Nat. Geogr. Mag.* 150: 160-173.
- URQUHART, F. A. & N. R. URQUHART. 1976. The overwintering site of the eastern population of the monarch butterfly (*Danaus p. plexippus*; Danaidae) in southern Mexico. *J. Lepid. Soc.* 30: 153-158.
- URQUHART, F. A., N. R. URQUHART, & F. MUNGER. 1970. A study of a continuously breeding population of *Danaus plexippus* in southern California compared to a migratory population and its significance in the study of insect movement. *J. Res. Lep.* 7: 169-181.
- WASSERTHAL, L. T. 1975. The role of butterfly wings in regulation of body temperature. *J. Insect Physiol.* 21: 1921-1930.
- WILLIAMS, C. B. 1930. The migration of butterflies. Oliver and Boyd, Edinburgh. xii + 473 p.
- WILLIAMS, C. B., G. F. COCKBILL, M. E. GIBBS, & J. A. DOWNES. 1942. Studies in the migration of Lepidoptera. *Trans. Roy. Entomol. Soc. Lond.* 92 (Part 1): 101-283.